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Dynamics of the density dependent predator–prey system with Beddington–DeAngelis functional response [☆]

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ABSTRACT

Two models of a density dependent predator–prey system with Beddington–DeAngelis functional response are systematically considered. One includes the time delay in the functional response and the other does not. The explorations involve the permanence, local asymptotic stability and global asymptotic stability of the positive equilibrium for the models by using stability theory of differential equations and Lyapunov functions. For the permanence, the density dependence for predators is shown to give some negative effect for the two models. Further the permanence implies the local asymptotic stability for a positive equilibrium point of the model without delay. Also the global asymptotic stability condition, which can be easily checked for the model is obtained. For the model with time delay, local and global asymptotic stability conditions are obtained.

1. Introduction

Stability of ecological systems is one of the most important and interesting topics in mathematical ecology. Skalski and Gilliam [19] present statistical evidence from 19 predator–prey systems that three predator-dependent functional response (Beddington–DeAngelis, Crowley–Martin, and Hassell–Varley) can provide better description of predator feeding over a range of predator–prey abundances. In some cases, the Beddington–DeAngelis type preformed better among them. Their most salient finding is that predator dependence in the functional response is a nearly ubiquitous property of the published date sets. Although the predator-dependent models that they considered fit those date reasonably well, not single functional response best describes all of the data sets. Theoretical studies have shown that the dynamics of models with predator-dependent functional responses can differ considerably from those with prey-dependent functional responses [12,13,17].

The predator–prey system with the Beddington–DeAngelis functional response

$$x' = x\left(a - bx - \frac{cy}{m_1 + m_2 x + m_3 y}\right), \qquad y' = y\left(-d + \frac{fx}{m_1 + m_2 x + m_3 y}\right), \tag{1.1}$$

was originally proposed by Beddington [1] and DeAngelis [7], independently. In the last years, some experts have studied the system [3,4,6,8,9,11,14,16].

Further, the certain environment confines for the predator to be density dependent. The theories on the model of the predator–prey relationship in which the predator has density dependence are not perfect[13,17]. Kartina [12] shows that predator dependence is important at not only very high predator densities on per capita predation rate but also at low

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predator densities. In ecology, we should consider both prey and predator density dependence, and need to take into account realistic levels of predator dependence. The qualitative analysis for the model will be difficult compared to the model with only density dependent prey [13,17].

In the present article, we deal with two different models with both Beddington–DeAngelis functional response and density dependent predator. These systems are described below.

Model 1: The first model describes the growth of a prey $x(t)$ and predator $y(t)$ with density dependence and is given

$$\begin{cases} x' = x\left(a - bx - \dfrac{cy}{m_1 + m_2x + m_3y}\right), \\ y' = y\left(-d - ey + \dfrac{fx}{m_1 + m_2x + m_3y}\right), \end{cases} \tag{1.2}$$

where all parameters are positive. For a thorough biological background of the model (1.2), see [1,7]. e stands for predator density dependence rate; the biological meanings of the other parameters are explicitly explained in Dimitrov and Kojouharov [8] and Liu and Beretta [14].

The initial conditions for the above system take the form of

$$x(0) > 0, \qquad y(0) > 0. \tag{1.3}$$

When $m_2 = m_3 = 0$ and $m_1 > 0$, (1.2) is reduced to Lotka–Volterra model.

When $m_1 = m$, $m_2 = 1$, $m_3 = 0$, system (1.2) will be the traditional Kolmogorov type predator–prey model with Holling type II functional response

$$x' = x\left(a - bx - \frac{cy}{m + x}\right), \qquad y' = y\left(-d - ey + \frac{fx}{m + x}\right), \tag{1.4}$$

and its various generalized forms have received great attention from both theoretical and mathematical biologists, and have been well studied.

When $m_1 = 0$, $m_2 = 1$, $m_3 = m$, system (1.2) will be the following ratio-dependent predator–prey model:

$$x' = x\left(a - bx - \frac{cy}{my + x}\right), \qquad y' = y\left(-d - ey + \frac{fx}{my + x}\right), \tag{1.5}$$

which incorporates mutual interference among predators. (1.5) has been studied by many authors and seen great progress, see Li and Takeuchi [13].

Model 2: Naturally, more realistic and interesting models of population interactions should take into account the effects of time delay [10,15,21,22]. Therefore, it is interesting and important to study the following delayed predator–prey model with the Beddington–DeAngelis functional response

$$\begin{cases} x' = x\left(a - bx - \dfrac{cy}{m_1 + m_2x + m_3y}\right), \\ y' = y\left(-d - ey + \dfrac{fx(t-\tau)}{m_1 + m_2x(t-\tau) + m_3y(t-\tau)}\right), \end{cases} \tag{1.6}$$

where the positive constant τ denotes the delay in the conversion of prey to predator, in other words, the delay in growth response of the predator. The biological meanings of the other parameters are the same as the system (1.2).

The initial conditions for the above delayed system take the form of

$$x_0(\theta) = \phi_1(\theta) \geqslant 0, \qquad y_0(\theta) = \phi_2(\theta) \geqslant 0, \quad \theta \in [-\tau, 0],\ x(0) > 0,\ y(0) > 0, \tag{1.7}$$

where $\phi = (\phi_1, \phi_2) \in C([-\tau, 0], R_+^2)$, $R_+^2 = \{(x, y)\colon\ x \geqslant 0,\ y \geqslant 0\}$, and $\|\phi\| = \max\{|\phi(\theta)|\colon\ \theta \in [-\tau, 0]\}$, and $|\phi|$ is any norm in R_+^2. As usual, we use the conventional notation $x_t(\theta) = x(t + \theta)$, for $\theta \in [-\tau, 0]$.

When $e = 0$, (1.6) was considered in [10,15]. When $e = m_2 = m_3 = 0$, (1.6) expresses Lotka–Volterra delay model and was studied in [21]. Further, (1.6) with $e = 0 = m_3 = 0$ (Holling type II functional response) was studies in [22]. When $m_1 = 0$, $m_2 = m$, $m_3 = 1$, system (1.6) will be the following delayed ratio-dependent predator–prey model:

$$x' = x\left(a - bx - \frac{cy}{mx + y}\right), \qquad y' = y\left(-d - ey + \frac{fx(t-\tau)}{mx(t-\tau) + y(t-\tau)}\right), \tag{1.8}$$

which has been studied, see Lu and Li [17].

In the following, we say an equilibrium of systems (1.2) and (1.6) is globally asymptotically stable if it is stable and attracts all positive solutions of systems (1.2) and (1.6), respectively.

The paper is organized as follows. In Section 2, we present sufficient conditions for permanence or non-permanence for two models. In Section 3, we obtain sufficient condition for the local or global asymptotic stability of a positive equilibrium of Model 1. In Section 4, we consider local or global asymptotic stability of Model 2. We conclude this article with a discussion in Section 5.

2. Permanence and non-permanence

In the following, a positive equilibrium of (1.2) and (1.6) is denoted as $E^*(x^*, y^*)$. Note that $E^*(x^*, y^*)$ satisfies the following algebraic equations

$$\begin{cases} (a - bx^*)(m_1 + m_2 x^* + m_3 y^*) - cy^* = 0, \\ (-d - ey^*)(m_1 + m_2 x^* + m_3 y^*) + fx^* = 0. \end{cases}$$

We can show by considering the graphs of the equations, if the condition

$$(f - dm_2)\frac{a}{b} > dm_1 \tag{H_0}$$

holds, then system (1.2) and (1.6) have a positive equilibrium.

Definition 2.1. System (1.2) or (1.6) is said to be permanent if there exist positive constants δ, Δ, with $0 < \delta \leqslant \Delta$ such that

$$\min\Big\{\liminf_{t\to+\infty} x(t), \liminf_{t\to+\infty} y(t)\Big\} \geqslant \delta, \qquad \max\Big\{\limsup_{t\to+\infty} x(t), \limsup_{t\to+\infty} y(t)\Big\} \leqslant \Delta$$

for all solutions of (1.2) or (1.6) with positive initial values. System (1.2) or (1.6) is said to be nonpermanent if there is a positive solution $(x(t), y(t))$ of (1.2) or (1.6) satisfying

$$\min\Big\{\limsup_{t\to+\infty} x(t), \limsup_{t\to+\infty} y(t)\Big\} = 0.$$

Theorem 2.1. *If system* (1.2) *satisfies one of the following two conditions*

$$\begin{cases} \text{(i) } f > dm_2 \text{ and } (f - dm_2)(\frac{a}{b} - \frac{c}{bm_3} - \frac{dm_3}{em_2}) > dm_1, \\ \text{or} \\ \text{(ii) } am_3 > c + \frac{bdm_3^2}{em_2} \text{ and } (f - dm_2)(\frac{a}{b} - \frac{c}{bm_3} - \frac{dm_3}{em_2}) > dm_1, \end{cases} \tag{H_1}$$

then system (1.2) *is permanent.*

Proof. From system (1.2), we can obtain that

$$x' > x\left(a - bx - \frac{c}{m_3}\right),$$

hence we have when $am_3 > c$,

$$\liminf_{t\to+\infty} x(t) \geqslant b^{-1}\left(a - \frac{c}{m_3}\right) \equiv \underline{x}.$$

It is easy to see that, for system (1.2),

$$x' < x(a - bx)$$

which implies that

$$\limsup_{t\to+\infty} x(t) \leqslant \frac{a}{b} = K \equiv \bar{x}.$$

Further we have

$$y' < y\left(-d - ey + \frac{f}{m_2}\right)$$

and

$$\limsup_{t\to+\infty} y(t) \leqslant \frac{\frac{f}{m_2} - d}{e} \equiv \overline{y}$$

and for sufficiently large $t > 0$,

$$y' \geqslant y\left(-d - ey + \frac{f\underline{x}}{m_1 + m_2\underline{x} + m_3\overline{y}}\right)$$

hence we have

$$\liminf_{t\to+\infty} y(t) \geqslant \frac{\frac{f\underline{x}}{m_1+m_2\underline{x}+m_3\overline{y}} - d}{e} \equiv \underline{y} > 0.$$

We can see that the second condition in (i) or (ii) ensures that $\underline{y} > 0$ and the first in (i) ensures that $\overline{y} > 0$. When (i) is satisfied, we have the first condition in (ii), which implies that $am_3 > c$ ensuring that $\underline{x} > 0$. Similarly, condition (ii) ensures that $\underline{y} > 0$, $\overline{y} > 0$ and $\underline{x} > 0$. From the above analysis, when condition (H_1) holds, system (1.2) is permanent. This completes the proof of Theorem 2.1. □

Remark 2.1. Let us review the known results for system (1.2) with $e = 0$, but the other parameters are time dependent [6,9]. The conditions of permanence for the system in [9, Theorem 3.1] is $f > dm_2$ (or $am_3 > c$) and $(f - dm_2)(\frac{a}{b} - \frac{c}{bm_3}) > dm_1$. Corollary 2.1 in Cui and Takeuchi [6] improves this result and shows that the system is permanent under condition (H_0). Theorem 2.1 shows that the predator density dependence rate e gives some negative effect on permanence. Note that condition (H_1) implies (H_0). This naturally induces that the condition (H_1) can ensure not only permanence but also existence of a positive equilibrium point for system (1.2).

According to Definition 2.1, we obtain the following theorem:

Theorem 2.2. *If $f < dm_2$, then (1.2) is nonpermanent. Further $(K, 0)$ is globally asymptotically stable. Here $K = ab^{-1}$.*

Proof. For (1.2), we have $y'(t) < y(-d + \frac{f}{m_2})$, which implies that $\lim_{t\to+\infty} y(t) = 0$. Since $x'(t) \leqslant x(t)(a - bx(t))$, for any $\varepsilon \in (0, a)$, there exists $T = T(\varepsilon)$ such that for $t > T$,

$$x(t)\bigl(a - \varepsilon - bx(t)\bigr) \leqslant x'(t) \leqslant x(t)\bigl(a - bx(t)\bigr).$$

This shows that $\lim_{t\to+\infty} x(t) = ab^{-1} = K$. It is easy to check that the Jacobian evaluated at $(K, 0)$ has two negative eigenvalues $-a, -d + fK/(m_1 + m_2K)$. Note that the latter is always negative because of $f < dm_2$. This completes the proof. □

Remark 2.2. About Model 2, the conditions for the existence of a positive equilibrium point or for the permanence and non-permanence are the same for Model 1 (Theorem 2.1 and Theorem 2.2).

3. Stability for Model 1

Now let us consider the local stability of the positive equilibrium of (1.2).

Let $x(t) = x^* + X(t)$, $y(t) = y^* + Y(t)$, then linearized system of system (1.2) is

$$\begin{cases} X' = x^*F_xX(t) + x^*F_yY(t), \\ Y' = y^*G_xX(t) + y^*G_yY(t), \end{cases} \tag{3.1}$$

where

$$F_x = \frac{cm_2y^*}{(m_1 + m_2x^* + m_3y^*)^2} - b, \qquad F_y = -\frac{c(m_1 + m_2x^*)}{(m_1 + m_2x^* + m_3y^*)^2} < 0,$$
$$G_x = \frac{f(m_1 + m_3y^*)}{(m_1 + m_2x^* + m_3y^*)^2} > 0, \qquad G_y = -\frac{fm_3x^*}{(m_1 + m_2x^* + m_3y^*)^2} - e < 0.$$

We can see that if

$$b > \frac{cm_2y^*}{(m_1 + m_2x^* + m_3y^*)^2}, \tag{3.2}$$

then $F_x < 0$.

Theorem 3.1. *If (H_1) is satisfied, then the positive equilibrium point E^* of (1.2) is locally asymptotically stable.*

Proof. It is easy to show that E^* is locally asymptotically stable if $F_x < 0$ (i.e. if (3.2) is satisfied). We will show that (H_1) implies (3.2).

Since $m_1 + m_2x^* + m_3y^* = cy^*/(a - bx^*)$, (3.2) is equivalent to $bcy^* > m_2(a - bx^*)^2$. Further from the former equation, we have $y^* = (a - bx^*)(m_1 + m_2x^*)/(c - am_3 + bm_3x^*)$ and the last inequality is rewritten as

$$\frac{bc(a - bx^*)(m_1 + m_2x^*)}{c - am_3 + bm_3x^*} > m_2\bigl(a - bx^*\bigr)^2,$$

which gives

$$b^2m_2m_3{x^*}^2 - 2bm_2(am_3 - c)x^* + bcm_1 + am_2(am_3 - c) > 0.$$

Note that (H_1) implies $\underline{x} < x^* < \bar{x}$, that is, $a - bx^* > 0$ and $c - am_3 + bm_3x^* > 0$. Since the discriminant of the left-hand side is

$$D = b^2m_2^2(am_3 - c)^2 - b^2m_2m_3\big[bcm_1 + am_2(am_3 - c)\big] = -m_2b^2\big[cm_2(am_3 - c) + bcm_1m_3\big] < 0,$$

the above inequality holds true for any positive x^*. Note that from (H_1), $am_3 - c > 0$ holds. This completes the proof. □

Remark 3.1. Theorem 3.1 implies that a positive equilibrium point of (1.2) is always locally asymptotically stable under the permanence condition (H_1) (or more exactly, under the condition $am_3 > c$ and (H_0)).

Example 3.1. Let $a = 1$, $b = 0.6$, $c = 0.15$, $d = 0.02$, $e = 0.9$, $f = 0.1$, $m_1 = 0.1$, $m_2 = 0.2$, $m_3 = 0.3$, then the system (1.2) becomes

$$\begin{cases} x' = x\left(1 - 0.6x - \dfrac{0.15y}{0.1 + 0.2x + 0.3y}\right), \\ y' = y\left(-0.02 - 0.9y + \dfrac{0.1x}{0.1 + 0.2x + 0.3y}\right). \end{cases} \tag{3.3}$$

Since the parameters satisfy (H_1), the positive equilibrium point $E^*(x^*, y^*) = (1.508, 0.315)$ of (3.3) is locally asymptotically stable by Theorem 3.1.

Rewrite system (1.2) and

$$\begin{cases} x' = x\left[-b(x - x^*) + \dfrac{cy^*}{m_1 + m_2x^* + m_3y^*} - \dfrac{cy}{m_1 + m_2x + m_3y}\right], \\ y' = y\left[-e(y - y^*) + \dfrac{fx}{m_1 + m_2x + m_3y} - \dfrac{fx^*}{m_1 + m_2x^* + m_3y^*}\right]. \end{cases} \tag{3.4}$$

In order to study the global stability of positive equilibrium $E^*(x^*, y^*)$ of system (1.2), we consider the function

$$V(t) = x - x^* - x^*\ln\frac{x}{x^*} + \omega\left(y - y^* - y^*\ln\frac{y}{y^*}\right),$$

where ω is a positive constant chosen later. Denote

$$\Delta(x, y) = \big(m_1 + m_2x^* + m_3y^*\big)(m_1 + m_2x + m_3y).$$

The time derivative of $V(t)$ along (3.4) is given

$$V'(t)\big|_{(3.4)} = -b\big(x - x^*\big)^2 - \omega e\big(y - y^*\big)^2 - \frac{(cm_1 - \omega fm_1)(x - x^*)(y - y^*)}{\Delta(x, y)} + \frac{cm_2(x - x^*)(xy^* - x^*y)}{\Delta(x, y)} + \frac{\omega fm_3(y - y^*)(xy^* - x^*y)}{\Delta(x, y)}.$$

Note that there are two terms containing $xy^* - x^*y$ in the right-hand side of the above equation and

$$xy^* - x^*y = y^*\big(x - x^*\big) + x^*\big(y^* - y\big).$$

We obtain that

$$V'(t)\big|_{(3.4)} = -b\big(x - x^*\big)^2 - \omega e\big(y - y^*\big)^2 + \frac{cm_2y^*}{\Delta(x, y)}\big(x - x^*\big)^2 - \frac{\omega fm_3x^*}{\Delta(x, y)}\big(y - y^*\big)^2 + \frac{\omega fm_1 + \omega fm_3y^* - cm_1 - cm_2x^*}{\Delta(x, y)}\big(x - x^*\big)\big(y - y^*\big).$$

Choosing ω as

$$\omega\big(fm_1 + fm_3y^*\big) = \big(cm_1 + cm_2x^*\big),$$

gives that

$$V'(t)\big|_{(3.4)} = -\left[b - \frac{cm_2y^*}{\Delta(x, y)}\right]\big(x - x^*\big)^2 - \left[\omega e + \frac{\omega fm_3x^*}{\Delta(x, y)}\right]\big(y - y^*\big)^2.$$

Therefore, we have the following result:

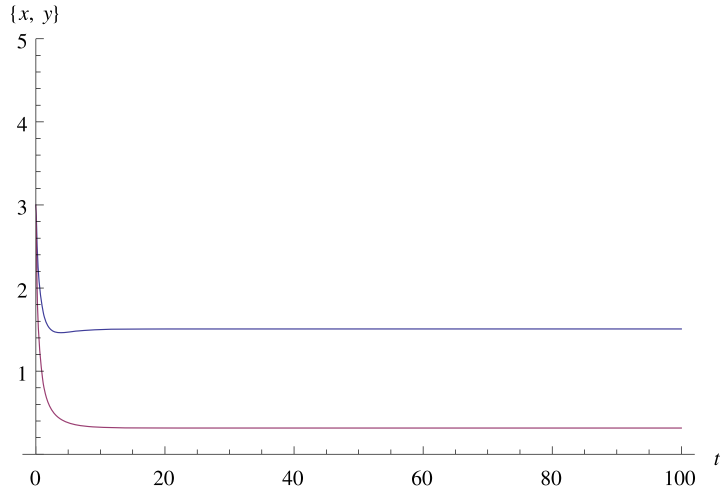

Fig. 1. The positive equilibrium (x^*, y^*) in system (1.2) is globally asymptotically stable when $a = 1$, $b = 0.6$, $c = 0.15$, $d = 0.02$, $e = 0.9$, $f = 0.1$, $m_1 = 0.1$, $m_2 = 0.2$, $m_3 = 0.3$, where the blue and red curves stand for $x(t)$ and $y(t)$, respectively.

Theorem 3.2. *If (H_1) holds and $b > \frac{cm_2 y^*}{\Delta(\underline{x}, \underline{y})}$, then the positive equilibrium $E^*(x^*, y^*)$ of system (1.2) is globally asymptotically stable in R_+^2.*

Remark 3.2. Fan and Kuang [9] gave several stability conditions for a bounded positive solution $(x^*(t), y^*(t))$ of (1.1) with time dependent coefficients. One of the stability conditions for the time independent case is

$$b > \frac{fm_1 + (cm_2 + fm_3)y^*}{\Delta(\underline{x}, \underline{y})}, \qquad \frac{fm_3 x^*}{\Delta(\bar{x}, \bar{y})} > \frac{c(m_1 + m_2 x^*)}{\Delta(\underline{x}, \underline{y})}$$

(see Theorem 2.4 in [9]). When all coefficients are constant and (1.1) includes the density dependence for predator (that is, $e \neq 0$), Theorem 3.2 shows that the above stability condition is improved.

Remark 3.3. From Theorem 3.1, E^* of (1.2) is always locally asymptotically stable under condition (H_1). Theorem 3.2 implies that E^* is globally asymptotically stable if we further assume

$$b > \frac{cm_2 y^*}{\Delta(\underline{x}, \underline{y})}. \tag{H_2}$$

Note that (H_2) is written as

$$b\bigl(m_1 + m_2 x^* + m_3 y^*\bigr)(m_1 + m_2 \underline{x} + m_3 \underline{y}) > cm_2 y^*.$$

Since $m_1 + m_2 x^* + m_3 y^* = cy^*/(a - bx^*)$, the above is equivalent to

$$x^* > \left[a - \frac{b}{m_2}(m_1 + m_2 \underline{x} + m_3 \underline{y})\right] \Big/ b.$$

Under (H_1), x^* is satisfied with $\underline{x} < x^* < \bar{x}$. Hence the above inequality holds true if

$$\underline{x} > \frac{1}{b}\left[a - \frac{b}{m_2}(m_1 + m_2 \underline{x} + m_3 \underline{y})\right].$$

Since $\underline{x} = (a - \frac{c}{m_3})/b$, the above is rewritten as

$$\frac{1}{b}\left(a - \frac{2c}{m_3}\right) > -\frac{1}{m_2}(m_1 + m_3 \underline{y}),$$

which is true if $a \geqslant 2c/m_3$.

Example 3.1 satisfies the above since $a - 2c/m_3 = 0$ and Theorem 3.2 shows that E^* of Example 3.1 is globally asymptotically stable.

Remark 3.4. Fig. 1 shows one example of the solution of (1.2) with the constants of Example 3.1, which converges to E^* as $t \to +\infty$.

4. Stability for Model 2

Let $x(t) = x^* + X(t)$, $y(t) = y^* + Y(t)$, then linearized system of system (1.6) is

$$\begin{cases} X' = x^* F_x X(t) + x^* F_y Y(t), \\ Y' = y^* G_x X(t-\tau) + y^* G_{y_1} Y(t-\tau) + y^* G_{y_2} Y(t). \end{cases} \tag{4.1}$$

Here F_x, F_y and G_x are the same as for (3.1) and $G_{y_1} + G_{y_2} = G_y$, where

$$G_{y_1} = -\frac{f m_3 x^*}{(m_1 + m_2 x^* + m_3 y^*)^2} < 0, \qquad G_{y_2} = -e < 0.$$

Let $F_x = -p$, $F_y = -q$, $G_x = -r$, $G_{y_1} = -s_1$, $G_{y_2} = -s_2$. If (H_1) holds, we have $p, q, s_1, s_2 > 0$ and $r < 0$ (see the proof of Theorem 3.1). Then, the characteristic equation is given by

$$\lambda^2 + \left(p x^* + s_1 y^* e^{-\lambda\tau} + s_2 y^*\right)\lambda + (p s_1 - q r) x^* y^* e^{-\lambda\tau} + p s_2 x^* y^* = 0. \tag{4.2}$$

Let $px^* + s_2 y^* = a_1 > 0$, $s_1 y^* = a_2 > 0$, $(ps_1 - qr)x^* y^* = a_4 > 0$, $ps_2 x^* y^* = a_3 > 0$, then Eq. (4.2) becomes

$$\lambda^2 + a_1\lambda + a_2\lambda e^{-\lambda\tau} + a_3 + a_4 e^{-\lambda\tau} = 0, \tag{4.3}$$

which has been extensively studied by many researchers (see, for example Ruan [18], Bellman and Cooke [2], Song and Wei [20]).

For $\tau = 0$, Eq. (4.3) becomes

$$\lambda^2 + (a_1 + a_2)\lambda + a_3 + a_4 = 0, \tag{4.4}$$

and

$$a_1 + a_2 > 0, \qquad a_3 + a_4 > 0,$$

hence, all roots of (4.4) have negative real parts.

We want to determine if the real part of some roots of (4.3) increases to reach zero and eventually becomes positive as τ varies. If $\lambda = i\omega$ is a root, then $\omega \neq 0$ (since $a_3 + a_4 > 0$) and

$$\begin{cases} -\omega^2 + a_2\omega \sin\omega\tau + a_4\cos\omega\tau + a_3 = 0, \\ a_1\omega + a_2\omega\cos\omega\tau - a_4\sin\omega\tau = 0, \end{cases} \tag{4.5}$$

thus, $(\omega^2 - a_3)^2 + a_1^2\omega^2 = a_2^2\omega^2 + a_4^2$, that is to say

$$\omega^4 + \left(a_1^2 - a_2^2 - 2a_3\right)\omega^2 - a_4^2 + a_3^2 = 0. \tag{4.6}$$

The roots of Eq. (4.6) are

$$\omega_\pm^2 = \frac{1}{2}\left(a_2^2 - a_1^2 + 2a_3\right) \pm \frac{1}{2}\left[\left(a_2^2 - a_1^2 + 2a_3\right)^2 - 4\left(a_3^2 - a_4^2\right)\right]^{\frac{1}{2}}. \tag{4.7}$$

Thus, if

$$a_2^2 - a_1^2 + 2a_3 < 0 \quad \text{and} \quad a_3^2 - a_4^2 > 0 \quad \text{or} \quad \left(a_2^2 - a_1^2 + 2a_3\right)^2 < 4\left(a_3^2 - a_4^2\right), \tag{H_3}$$

then neither ω_+^2 nor ω_-^2 is positive, that is (4.6) does not have positive roots. Therefore, characteristic equation (4.3) does not have purely imaginary roots. Since all roots of (4.4) have negative real parts, by Rouche's theorem, it follows that the roots of (4.3) have negative real parts too. This can be summarized as follows.

Lemma 4.1. *If (H_1) and (H_3) hold, then all roots of (4.3) have negative real parts for all $\tau > 0$.*

On the other hand, if

$$a_3^2 - a_4^2 < 0 \quad \text{or} \quad a_2^2 - a_1^2 + 2a_3 > 0 \quad \text{and} \quad \left(a_2^2 - a_1^2 + 2a_3\right)^2 = 4\left(a_3^2 - a_4^2\right), \tag{H_4}$$

then (4.6) has a positive root ω_+^2 and if

$$a_3^2 - a_4^2 > 0, \qquad a_2^2 - a_1^2 + 2a_3 > 0 \quad \text{and} \quad \left(a_2^2 - a_1^2 + 2a_3\right)^2 > 4\left(a_3^2 - a_4^2\right), \tag{H_5}$$

then (4.6) has two positive roots $\omega_\pm^2$. In both cases, (4.3) has purely imaginary roots when τ takes certain values. These critical values $\tau_j^\pm$ of τ can be determined from system (4.5), given by

$$\tau_j^\pm = \frac{1}{\omega_\pm}\arccos\left\{\frac{a_4(\omega_\pm^2 - a_3) - a_1 a_2\omega_\pm^2}{a_2^2\omega_\pm^2 + a_4^2}\right\} + \frac{2j\pi}{\omega_\pm}, \quad j = 0, 1, 2, \ldots. \tag{4.8}$$

From the above analysis we have the following lemma.

Lemma 4.2.

(i) *If* (H_1) *and* (H_4) *hold and* $\tau = \tau_j^+$, *then* (4.3) *has a pair of purely imaginary roots* $\pm i\omega_+$.
(ii) *If* (H_1) *and* (H_5) *hold and* $\tau = \tau_j^+$ $(\tau = \tau_j^-$ *respectively*), *then* (4.3) *has a pair of purely imaginary roots* $\pm i\omega_+$ ($\pm i\omega_-$ *respectively*).

Then we would expect that the real part of some roots to (4.3) becomes positive when $\tau > \tau_j^+$ and $\tau < \tau_j^-$. To see if it is the case, denote

$$\lambda_j^\pm = \alpha_j^\pm(\tau) + i\omega_j^\pm(\tau), \quad j = 0, 1, 2, \dots,$$

and the root of (4.3) satisfying

$$\alpha_j^\pm\left(\tau_j^\pm\right) = 0, \qquad \omega_j^\pm\left(\tau_j^\pm\right) = \omega_\pm.$$

We can verify that the following transversality conditions hold:

$$\frac{d}{d\tau} Re\,\lambda_j^+\left(\tau_j^+\right) > 0, \qquad \frac{d}{d\tau} Re\,\lambda_j^-\left(\tau_j^-\right) < 0.$$

It follows that $\tau_j^\pm$ are bifurcation values. Thus, we have the following theorem about the distribution of the characteristic roots of (4.3).

Theorem 4.1. *Let* $\tau_j^\pm$ $(j = 0, 1, 2, \dots)$ *be defined by* (4.8).

(i) *If* (H_1) *and* (H_3) *hold, then all roots of* (4.3) *have negative real parts for all* $\tau \geqslant 0$.
(ii) *If* (H_1) *and* (H_4) *hold, then when* $\tau \in [0, \tau_0^+)$ *all roots of* (4.3) *have negative real parts, when* $\tau = \tau_0^+$, (4.3) *has a pair of purely imaginary roots* $\pm i\omega_+$, *and when* $\tau > \tau_0^+$, (4.3) *has at least one root with positive real part.*
(iii) *If* (H_1) *and* (H_5) *hold, then there is a positive integer k such that there are k switches from stability to instability to stability*; *that is, when*

$$\tau \in \left[0, \tau_0^+\right],\ \left(\tau_0^-, \tau_1^+\right),\ \dots,\ \left(\tau_{k-1}^-, \tau_k^+\right),$$

all roots of (4.3) *have negative real parts, and when*

$$\tau \in \left[\tau_0^+, \tau_0^-\right),\ \left[\tau_1^+, \tau_1^-\right),\ \dots,\ \left[\tau_{k-1}^+, \tau_{k-1}^-\right) \quad and \quad \tau > \tau_k^+,$$

(4.3) *has at least one root with positive real part.*

Remark 4.1. Theorem 4.1 (iii) shows the delay τ passes through a critical values τ_j^+, $j = 0, 1, 2, \dots, k-1$, the interior equilibrium $E^*(x^*, y^*)$ for system (1.6) loses its stability and Hopf bifurcation occurs.

Remark 4.2. We should mention that the main part of Theorem 4.1 was obtained by Cooke and Grossman [5] in analyzing a general second-order equation with delayed friction and delayed restoring force.

Example 4.1. In system (1.6), if the values of constants a, b, c, d, e, f, m_1, m_2, m_3 are the same as Example 3.1, we can calculate

$$a_1 = \left[b - \frac{cm_2 y^*}{(m_1 + m_2 x^* + m_3 y^*)^2}\right] x^* + e y^* \approx 1.130,$$
$$a_2 = \frac{f m_3 x^* y^*}{(m_1 + m_2 x^* + m_3 y^*)^2} \approx 0.058,$$
$$a_3 = \left[b - \frac{cm_2 y^*}{(m_1 + m_2 x^* + m_3 y^*)^2}\right] e x^* y^* \approx 0.240,$$
$$a_4 = \left\{\left[b - \frac{cm_2 y^*}{(m_1 + m_2 x^* + m_3 y^*)^2}\right] \frac{f m_3 x^*}{(m_1 + m_2 x^* + m_3 y^*)^2} + \frac{cf(m_1 + m_2 x^*)(m_1 + m_3 y^*)}{(m_1 + m_2 x^* + m_3 y^*)^4}\right\} x^* y^* \approx 0.058,$$
$$a_3^2 - a_4^2 \approx 0.054 > 0,$$
$$a_2^2 - a_1^2 + 2a_3 \approx -0.794 < 0.$$

Together with Example 3.1, the conditions (H_1) and (H_3) are satisfied, which shows the local asymptotic stability of E^* of system (1.6) by Theorem 4.1 for any $\tau \geqslant 0$.

Rewrite system (1.6) as follows

$$\begin{cases} x' = x\left[-b(x-x^*) + \dfrac{cy^*}{m_1+m_2x^*+m_3y^*} - \dfrac{cy}{m_1+m_2x+m_3y}\right], \\ y' = y\left[-e(y-y^*) + \dfrac{fx(t-\tau)}{m_1+m_2x(t-\tau)+m_3y(t-\tau)} - \dfrac{fx^*}{m_1+m_2x^*+m_3y^*}\right]. \end{cases} \tag{4.9}$$

In order to study the global stability of positive equilibrium $E^*(x^*, y^*)$ of system (1.6), we consider the functional

$$V(t) = \omega_1 \int_0^{x-x^*} \frac{s}{s+x^*}\,ds + \omega_2 \int_0^{y-y^*} \frac{s}{s+y^*}\,ds + \frac{\omega_2 f(m_1+m_3y^*)}{2\beta} \int_{t-\tau}^{t} \big(x(s)-x^*\big)^2\,ds$$
$$+ \frac{\omega_2 f m_3 x^*}{2\beta} \int_{t-\tau}^{t} \big(y(s)-y^*\big)^2\,ds.$$

Here ω_1 and ω_2 are positive constants chosen later and $\alpha = \Delta(\bar{x}, \bar{y})$, $\beta = \Delta(\underline{x}, \underline{y})$, where

$$\Delta(x, y) = \big(m_1+m_2x^*+m_3y^*\big)(m_1+m_2x+m_3y).$$

Further define $\gamma = f(m_1+m_3y^*)/(b\beta - cm_2y^*)$, which is positive, if $b\beta > cm_2y^*$. Note that $b\beta > cm_2y^*$ is equivalent to (H_2).

The time derivative of $V(t)$ along (4.9) is given

$$\begin{aligned} V'(t)\big|_{(4.9)} &= -b\omega_1\big(x-x^*\big)^2 - \frac{c\omega_1 m_1}{\Delta(x,y)}\big(x-x^*\big)\big(y-y^*\big) + \frac{c\omega_1 m_2}{\Delta(x,y)}\big(x-x^*\big)\big(xy^*-x^*y\big) - e\omega_2\big(y-y^*\big)^2 \\ &\quad + \frac{f\omega_2 m_1}{\Delta(x(t-\tau), y(t-\tau))}\big(x(t-\tau)-x^*\big)\big(y-y^*\big) \\ &\quad + \frac{f\omega_2 m_3}{\Delta(x(t-\tau), y(t-\tau))}\big(y-y^*\big)\big(x(t-\tau)y^*-x^*y(t-\tau)\big) \\ &\quad + \frac{\omega_2 f(m_1+m_3y^*)}{2\beta}\big(x-x^*\big)^2 - \frac{\omega_2 f(m_1+m_3y^*)}{2\beta}\big(x(t-\tau)-x^*\big)^2 \\ &\quad + \frac{\omega_2 f m_3 x^*}{2\beta}\big(y-y^*\big)^2 - \frac{\omega_2 f m_3 x^*}{2\beta}\big(y(t-\tau)-y^*\big)^2. \end{aligned}$$

Noting that the terms xy^*-x^*y and $x(t-\tau)y^*-x^*y(t-\tau)$ in the right-hand side of the above equation can be expressed as

$$xy^*-x^*y = y^*\big(x-x^*\big) + x^*\big(y^*-y\big)$$

and

$$x(t-\tau)y^*-x^*y(t-\tau) = y^*\big(x(t-\tau)-x^*\big) + x^*\big(y^*-y(t-\tau)\big)$$

gives

$$\begin{aligned} V'(t)\big|_{(4.9)} &= -\left(b\omega_1 - \frac{c\omega_1 m_2 y^*}{\Delta(x,y)}\right)\big(x-x^*\big)^2 - \frac{c\omega_1(m_1+m_2x^*)}{\Delta(x,y)}\big(x-x^*\big)\big(y-y^*\big) - e\omega_2\big(y-y^*\big)^2 \\ &\quad + \frac{f\omega_2(m_1+m_3y^*)}{\Delta(x(t-\tau), y(t-\tau))}\big(x(t-\tau)-x^*\big)\big(y-y^*\big) - \frac{f\omega_2 m_3 x^*}{\Delta(x(t-\tau), y(t-\tau))}\big(y(t-\tau)-y^*\big)\big(y-y^*\big) \\ &\quad + \frac{\omega_2 f(m_1+m_3y^*)}{2\beta}\big(x-x^*\big)^2 - \frac{\omega_2 f(m_1+m_3y^*)}{2\beta}\big(x(t-\tau)-x^*\big)^2 \\ &\quad + \frac{\omega_2 f m_3 x^*}{2\beta}\big(y-y^*\big)^2 - \frac{\omega_2 f m_3 x^*}{2\beta}\big(y(t-\tau)-y^*\big)^2 \\ &\leqslant -\left(b\omega_1 - \frac{c\omega_1 m_2 y^*}{\Delta(x,y)} - \frac{\omega_2 f(m_1+m_3y^*)}{2\beta}\right)\big(x-x^*\big)^2 - \frac{c\omega_1(m_1+m_2x^*)}{\Delta(x,y)}\big(x-x^*\big)\big(y-y^*\big) \\ &\quad - \left(e\omega_2 - \frac{\omega_2 f(m_1+m_3y^*)}{2\beta} - \frac{\omega_2 f m_3 x^*}{\beta}\right)\big(y-y^*\big)^2, \end{aligned}$$

where we used the inequality $ab \leqslant (a^2+b^2)/2$.

Choose $\omega_1 = \gamma\omega_2$, and if $\rho = e - f(m_1 + m_3 y^* + 2m_3 x^*)/2\beta > 0$, then V' is negative definite if,

$$\left(\frac{c\omega_1(m_1 + m_2 x^*)}{\beta}\right)^2 < 4\left(b\omega_1 - \frac{c\omega_1 m_2 y^*}{\beta} - \frac{\omega_2 f(m_1 + m_3 y^*)}{2\beta}\right)\omega_2\rho$$

that is

$$c^2\big(m_1 + m_2 x^*\big)^2 f\big(m_1 + m_3 y^*\big) < 2\beta\rho\big(b\beta - cm_2 y^*\big)^2.$$

Therefore, we have the following result:

Theorem 4.2. *If* (H_1), (H_2) *and the following conditions*

(i) $\rho = e - f(m_1 + m_3 y^* + 2m_3 x^*)/2\beta > 0$,
(ii) $c^2(m_1 + m_2 x^*)^2 f(m_1 + m_3 y^*) < 2\beta\rho(b\beta - cm_2 y^*)^2$

hold, then the positive equilibrium $E^*(x^*, y^*)$ *of system* (1.6) *is globally asymptotically stable in* R^2_+ *for any* $\tau > 0$.

Remark 4.3. Theorem 3.2 shows that E^* of (1.2) is globally asymptotically stable under conditions (H_1) and (H_2). Hence, Theorem 4.2 implies that for the global asymptotic stability of E^* of (1.6) under any time delay $\tau > 0$, the additional conditions (i) and (ii) are needed.

Example 4.2. In system (1.6), if the values of constants a, b, c, d, e, f, m_1, m_2, m_3 are the same as Example 3.1, we can calculate

$$\begin{aligned}
&\beta = \big(m_1 + m_2 x^* + m_3 y^*\big)(m_1 + m_2\underline{x} + m_3\underline{y}) \approx 0.161,\\
&b\beta - cm_2 y^* \approx 0.087 > 0,\\
&\rho = e - \frac{f(m_1 + m_3 y^* + 2m_3 x^*)}{2\beta} \approx 0.559 > 0,\\
&c^2\big(m_1 + m_2 x^*\big)^2 f\big(m_1 + m_3 y^*\big) - 2\beta\rho\big(b\beta - cm_2 y^*\big)^2 \approx -0.001 < 0.
\end{aligned}$$

Since (H_1), (H_2) and (i)–(ii) of Theorem 4.2 are satisfied, E^* is globally asymptotically stable for any $\tau > 0$.

5. Discussion

In this paper, we have considered two models for density dependent prey–predator with Beddington–DeAngelis functional response. Model 1 does not include the time delay in the functional response and Model 2 does. Both Model 1 and Model 2 include the density dependence for predator. On permanence for both models, Theorem 2.1 shows that the density dependence for predator gives some negative effect, compared to the models without the density dependence. Further this permanence condition (H_1) implies the local asymptotic stability to a positive equilibrium point for Model 1. We also proved that some easily verifiable condition (H_2) with (H_1) ensures for the positive equilibrium of Model 1 to be globally asymptotically stable. The condition (H_2) improves the known condition for the model without density dependence for predator. We further gave the global asymptotic stability conditions for Model 2, which include some additional conditions for the parameter except for global stability condition (H_1) and (H_2) for Model 1.

Let us compare our results for the system with Beddington–DeAngelis functional response on permanence, local and global asymptotic stability to the system with Lotka–Volterra interaction or Holling type II functional response or ratio-dependent functional response. It is well known that Lotka–Volterra system ((1.2) with $m_2 = m_3 = 0$) has a positive equilibrium point under (H_0), which also ensures permanence and global asymptotic stability of a positive equilibrium point. Our result shows that also for (1.2) with Beddington–DeAngelis functional response, (H_0) ensures the existence of a positive equilibrium point. But for permanence or local (or global) asymptotic stability of the point, we need (H_1) (or (H_2)), which is stronger than (H_0). Now let us compare our results to the known results for Holling type II ((1.2) with $m_3 = 0$). For the existence of a positive equilibrium point, (H_0) is a necessary and sufficient condition both for Holling type II and Beddington–DeAngelis response. It is known that a positive equilibrium point of the system with Holling type II becomes unstable when the carrying capacity a/b increases and e is small. Theorems 3.1 and 3.2 imply that the positive equilibrium point E^* of (1.2) remains to be locally or globally asymptotically stable under large carrying capacity. We also compare our results to the results for ratio-dependent case ((1.2) with $m_1 = 0$, $m_2 = 1$, $m_3 = m$). H. Li [13] proved that the system with ratio-dependent functional response is permanent and its positive equilibrium is locally asymptotically stable if (H_1) with $m_1 = 0$ is satisfied. Further [13] showed the global asymptotic stability of the point is ensured under (H_1) and (H_2) with $m_1 = 0$.

On the stability of Model 2, Theorem 4.1 gives the condition for its positive equilibrium point E^* to be locally asymptotically stable under any time delay $\tau > 0$. We cannot find an example of unstable E^*. This suggests us that E^* is always locally asymptotically stable for any $\tau > 0$ under the permanence condition (H_1). That is, (H_3) holds true if (H_1) is satisfied, more exactly, $a_2^2 - a_1^2 + 2a_3$ is always negative under (H_1). Hence, our conjecture is as follows:

Conjecture. *A positive equilibrium point of Model* 2 *is locally asymptotically stable for any* $\tau > 0$ *if* (H_1) *is satisfied.*

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